



## Archival electronic tagging of a predatory sea star – Testing a new technique to study movement at the individual level

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### ABSTRACT

Sea stars are important marine predators, and their feeding often controls the distribution of associated species. Therefore, quantifying their activity at an individual level is important in further understanding how they structure marine communities. Sea stars are difficult to tag, so there is little information on activity of sea stars in their natural environment over extended periods of days to weeks. We tagged the New Zealand sea star *Coscinasterias muricata* with small archival electronic tags that recorded water temperature and depth every 5 min for up to 2 weeks. The tagging was undertaken to test the viability of using electronic tags in research on the ecology of the sea stars in a New Zealand fiord, where their vertical distribution is influenced by the presence of low-salinity layers. The effects of the tagging were tested in the laboratory and in the field, with tagging having no detectable influence on *in vitro* survival, feeding rate, and righting time, or on their *in situ* movement and depth distribution. Laboratory experiments testing the salinity tolerance of *C. muricata* showed they could tolerate salinities as low as 25 PSU for at least a 20-day period. Tagging of sea stars in their natural environment provided information on depth distributions, vertical migrations and the influence of the physical environment on their behaviour. The tagging also revealed a large variation in activity at the individual level. This study represents one of the first to utilise electronic tagging to study the ecology of a mobile invertebrate such as a sea star. The success of this initial study suggests that we could gain valuable quantitative insight into the ecology of these animals in future tag deployments.

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### 1. Introduction

Electronic tagging of marine species has been undertaken for nearly 50 years (Sibert and Nielsen, 2000), providing information on movement and migration, behaviour and physiology of organisms in their natural environment that would otherwise be difficult to quantify. Electronic tagging of marine species has largely focused on finfish and other marine vertebrates (e.g., marine mammals) for reasons such as their economic importance, large size, and an interest in physiology (Arnold and Dewar, 2001; Block et al., 2005; Davis et al., 2007). Fewer studies have involved tagging marine invertebrates. For example, in 1998 an estimated 11,800 electronic tags were placed on marine animals, of which only ~35 were reported as being used on marine invertebrates (Stone et al., 1999).

Electronic tagging of marine invertebrates has included non-archival tagging (tags that identify an individual but do not record any information during deployment) such as PIT (passive integrated transponder) tags and active transponder tags to remotely track animal movements. PIT tags have been tested for use with sea urchins (Hagen, 1995) and benthic octopus (Anderson and Babcock, 1999), while movements of marine decapod crustaceans fitted with trans-

ponders have been tracked in a number of species (Phillips et al., 1984; Smith et al., 1998). Archival tagging, where data such as temperature and depth is recorded and logged by the tag during deployment, has been restricted to studies on decapod crabs (Freire and González-Gurrirarán, 1998) and squid (Semmens et al., 2007). An excellent example of the utilisation of archival tags was undertaken on the jumbo squid *Dosidicus gigas* (Gilly et al., 2006), with researchers able to fully understand and appreciate the complex migration behaviour and space utilisation of this animal in its natural environment.

The latest technology in microcomputers and the miniaturization of waterproof archival tags opens up the possibility of electronically tagging a range of smaller benthic marine invertebrates. Marine invertebrates such as sea urchins and sea stars are often dominant grazers and predators in their environment (Power et al., 1996), and their feeding behaviour can have profound effects on their environment (such as zonation patterns and habitat conversion, Paine 1971, 1974). The utilisation of miniature archival tags provides a new and innovative approach to investigating movement and foraging behaviour of echinoderms and, in turn, has the potential to greatly advance our understanding of their ecological role in the marine environment. Additionally these organisms frequently inhabit physically dynamic seascapes along the coast; hence the approach will also provide insight into how benthic invertebrates respond to changes in their surrounding physical environment.

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Tagging of sea stars for individual recognition has been attempted using a number of methods including vital stains (Loosanoff, 1937; Feder, 1959, 1970; Kvalvågnaes, 1972), puncturing (Kvalvågnaes, 1972; Paine, 1976) and harnesses (Kvalvågnaes, 1972). In this study, we describe the first attempt to archival tag a shallow water, mobile marine invertebrate, in this case the New Zealand 11-armed sea star, *Coscinasterias muricata* Verrill (Asteroidea: Asteriidae). Echinoderms including *C. muricata* are known to play an important role in structuring benthic suspension-feeding communities in New Zealand fiords. The study involved laboratory testing for any detrimental effects of attaching the tag to the sea star, and field-testing of tags over a two-week period. The field study was undertaken in Doubtful Sound, one of 14 fiords along the southwest coast of New Zealand. The region has extremely high rainfall (~5 to 7 m year<sup>-1</sup>, up to 200 mm day<sup>-1</sup>) that results in the frequent presence of a buoyant low-salinity layer (LSL) that overlies the seawater (Gibbs, 2001). The LSL affects the vertical distribution of species directly through the exclusion of sessile stenohaline species from shallow waters (Grange et al., 1981; Kregting and Gibbs, 2006; Barker and Russell, 2008), and also indirectly by restricting predation of mobile stenohaline species on shallow water communities (Witman and Grange, 1998). The LSL is extremely dynamic and its thickness fluctuates in response to rain and wind events (Gibbs, 2001); hence the distribution of mobile predators such as *C. muricata* is ultimately linked with weather patterns and temporal changes in salinity stratification. Therefore, in this study, there is a wider interest in quantifying the role of salinity in controlling the small-scale movements and feeding behaviour of *C. muricata*.

## 2. Materials and methods

### 2.1. Study site

Tagging of *C. muricata* was made at Espinosa Point, Doubtful Sound (166° 58' 45" E, 45° 18' 00" S), one of 14 glacially-carved fiords that lie along the southwest coast of New Zealand. The hydrography of Doubtful Sound is complex. The fiord has a large input of freshwater, with an average rainfall of 465 mm month<sup>-1</sup>, an average riverine input of 135 m<sup>3</sup> s<sup>-1</sup> and an average anthropogenic input of ~380 m<sup>3</sup> s<sup>-1</sup> that is discharged into the sound from the Manapouri Hydroelectric Power Station (Gibbs et al., 2000; Gibbs, 2001). The fresh water input results in a semi-permanent low-salinity layer (LSL) throughout the fiord, which has typical salinities of 5–10‰. The LSL varies in thickness

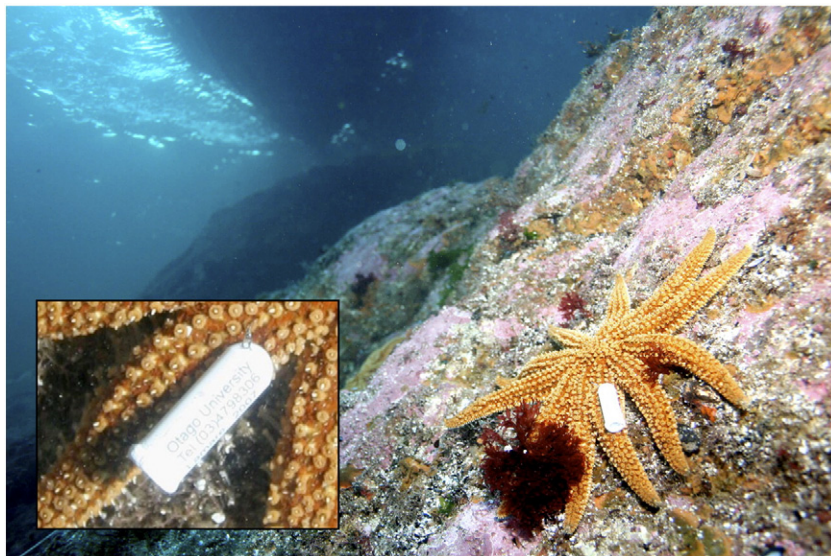
depending on location and on weather conditions, but in general is thicker toward the fiord head and during rain events. At Espinosa Point, LSL thickness (as defined by the depth of the 28 PSU isohaline) ranges from 0.5 to 3 m during dry periods to as great as 8–10 m during rain events. The tidal cycle at Espinosa Point is semi-diurnal and has a maximum vertical range of 2 m; organisms inhabiting the first few meters of the rock walls are therefore exposed to a wide range of salinity over the course of a tide cycle. Water temperatures within the LSL in Doubtful Sound range from about 7 °C to 18 °C, whereas temperatures within the seawater layer are more stable and range from about 11 °C to 17 °C annually.

Espinosa Point seabed consists of sloping schist bedrock to a depth of 15 m, which flattens off to a low sloping sandy fan. Based on a diver survey using a high resolution depth gauge and swimming a known distance, the slope of the rock wall was estimated at approximately 60° with a relief estimated at 1 m vertical distance to 2 m distance along the rock wall. In some places the bedrock is covered with small areas (<10 m<sup>2</sup>) of coarse sand, mussel shell fragments, and small schist and quartz rocks (30 to 70 cm diameter). There is strong zonation in the subtidal community with a dense band of the green algae *Ulva pertusa* and the blue mussel *Mytilus edulis galloprovincialis* extending from the low intertidal to a depth of 1 m (MLW). Below this is a patchy band of sea urchins *Evechinus chloroticus* extending from 1 m to 3 m depth, then a similarly patchy band of *C. muricata*. The vertical distribution of these two species is however, variable depending on the depth of the LSL. Encrusting coralline algae dominates the algal communities in the sea urchin band, with increasing amounts of articulate coralline algae below 3–4 m depth. Between 5 m and 15 m depth, the rock wall community is dominated by a species rich assemblage of suspension-feeding invertebrates (e.g., brachiopods, ascidians, black corals) and deeper water macroalgae such as *Carpophyllum flexuosum*, *Ecklonia radiata* and *Codium fragile*.

### 2.2. Tagging

Sea stars were tagged with small (13 mm × 38 mm, 5 g in water) archival temperate and pressure DST-milli™ electronic tags (Fig. 1) manufactured by Star-Oddi (Iceland). For deployment, tags were programmed to record sea temperature (0.032 °C resolution, ±0.1 °C accuracy) and depth (±0.4% accuracy) every 5 min.

Tags were attached to sea stars by piercing one arm ~10 mm from the central disk with 0.7 mm stainless steel wire (Fig. 1). The piercing was



**Fig. 1.** A tagged *C. muricata* (170 mm diameter) at Espinosa Point, Doubtful Sound. Insert shows the attachment of the Star-oddi DST-milli temperature/time/depth recorders to an arm of the sea star by piercing the arm with stainless steel wire.

directed through the mid-line of the arm, with the wire protruding through the oral side doubled back between the arms. The tags have a small attachment hole that the wire was threaded through, and both ends of the wire twisted together and the excess wire removed. This left the tag firmly hatched to the aboral surface of the sea star arm.

### 2.3. Effects of tagging on *C. muricata*

Experimental tests for any detrimental effects of tagging on feeding, righting, and *in situ* movement of *C. muricata* were undertaken. Effects of tagging on survival and the retention of tags were also monitored. Experimental tests for feeding and righting were carried out on animals that were collected at Espinosa Point and transported to the Portobello Marine Laboratory. Eight tanks with flow-through filtered seawater at ambient temperature were established, and to each three sea stars were randomly allocated. In four of the tanks, the sea stars were tagged with dummy tags of approximately the same dimensions and weight as the electronic tags. The sea stars in the four control tanks were left untagged. The mean size and weight of the sea star was not significantly different ( $P > 0.05$ ) between the two treatments. Sea stars were then fed 10 live cockles (*Austrovenus stutchburyi*) and over the following 5 days a daily count of the number of cockle eaten was recorded. Sea stars used in the feeding trials were also tested for righting rate at the beginning and end of the 5-day feeding trials. After any handling for tagging, weighing and measuring the sea stars were left to settle for 1 h then were placed upside down and the time taken to right was recorded. This was repeated for each sea star three times, with a five-minute break between trials.

Sixteen large *C. muricata* (~0.20 to 0.30 m in diameter) were collected from Espinosa Point, and half were tagged with dummy tags as described above. The remaining *C. muricata* were handled in a similar manner to the tagged sea stars but were not tagged. All sea stars were transported a site of similar aspect to the shore and topography but largely devoid of *C. muricata*, and released by divers at a depth of 5 m within a 1 m<sup>2</sup> area. The site was revisited 24 h later and the distance travelled from the original release location, and the depth of the tagged and untagged sea stars was recorded.

### 2.4. Effects of salinity on *C. muricata* activity

The vertical distribution of *C. muricata* in Doubtful Sound is known to be influenced by gradients in salinity (Witman and Grange, 1998). A series of laboratory experiments were therefore conducted in order to isolate the effects of salinity on sea star activity. *C. muricata* were collected from Espinosa Point and kept in 110 L aquaria supplied with running seawater for 3 weeks and fed a diet of bivalves prior to experimentation. The sea stars were then divided into five groups and subjected to one of five salinity treatments, 33–34 PSU (control), 30 PSU, 25 PSU, 20 PSU and 15 PSU. Treatments were applied in a flow-through aquaria system, with freshwater and seawater mixed in a reservoir manifold that then fed water into the treatment tanks (each treatment having its own mixing manifold). The desired salinity was obtained by varying the flow of freshwater and seawater into each manifold. Each treatment was replicated three times, with each replicate having three sea stars per tank.

The application of salinity treatments were made in a 20-day experiment, with the sea stars not acclimated to salinity treatments prior to the experiment. At the start of the treatment the righting time for each animal was recorded (in seconds) at 9:00 AM, 11:00 AM, 1:00 PM and 3:00 PM. On days 2, 3, 5, 10 and 20, the righting response was recorded at 10:30 AM and 1:30 PM. Righting time in seconds was divided by 1000 to give an activity coefficient (Shirley and Stickle, 1982).

### 2.5. Field deployment

Five large *C. muricata* of similar size (0.20 to 0.23 m total ray diameter) were collected by SCUBA and were tagged on 13 February

2008 using methods described above. The sea stars were then immediately returned to the location and depth from which they were collected. Tagging and return was completed within 1 h of collection. A short inspection dive was carried out the following day, and three of the five tagged sea stars were relocated and appeared normal (the remaining two were not found). Tags were relocated 2 weeks later (27 February 2008) and data was successfully retrieved for three of the five tagged sea stars. Two tags were relocated on the seafloor and one of the tags was found still attached to a sea star. The latter tag had flooded after 10 days; however, data for the 10-day period were still able to be retrieved from the tag.

To remove the effects of tide on the depth records of the sea stars, we moored one of the Mill-DST tags at 10 m depth, and programmed it to record tidal height every 5 min and at precisely the same time as readings were made by the tags deployed on sea stars. Later, the tidal signal was removed from the sea star recordings and the residual depth records of the tagged sea stars indicated their movement up and down the rock wall, and their depth relative to mean low water (MLW). There was a small degree of horizontal movement of the tagged sea stars, with individuals found within 5 m of their release point.

### 2.6. Characterising the physical environment

A mooring of conductivity/temperature recorders (Data Flow Systems Pty Ltd, New Zealand) was deployed at the study site during the period of the tagging trials. Recorders were placed at 2, 4, 6, 8 and 10 m depth and programmed to measure temperature ( $\pm 0.1$  °C) and salinity ( $\pm 0.1$  mSiemens cm<sup>-1</sup>) every 10 min. Temperature and salinity profiles for the upper 10 m of the water column were also recorded using a Seabird SE25 CTD profiler at the end of the deployment period (27 February 2008). Hourly rainfall data (mm h<sup>-1</sup>) were obtained from a weather station located at the entrance of Doubtful Sound (45°13' S, 166°53' E).

### 2.7. Statistical analysis

The effects of tagging on sea star behaviour and physiology were examined using ANOVA, while the effect of salinity on sea star activity was tested using repeated measures ANOVA. If required, data were log or  $\log(x + 1)$  transformed prior to testing, with homogeneity of variance examined using a Bartlett test (Bartlett, 1937). In one case, it was not possible to homogenise variances, and comparisons were made using Welsh ANOVA test. All statistical analyses were undertaken using JMP 7.0 (SAS Institute Inc.).

## 3. Results

### 3.1. Effects of tagging on *C. muricata*

During feeding and righting experiments, all sea stars tagged using the method described above retained their tags over a two-week period. There was no mortality in either the tagged or untagged sea stars over this period. Repeated measures ANOVA indicated that there

**Table 1**

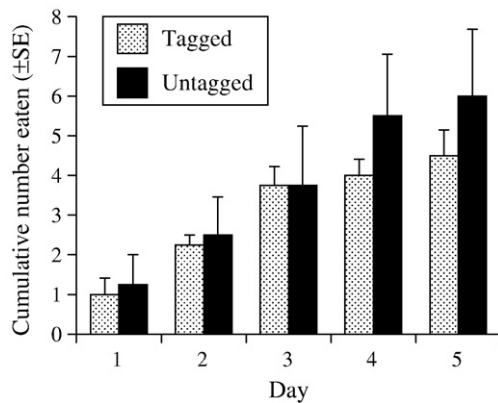
Univariate repeated measures ANOVA of the number of cockles eaten between tagged and untagged *C. muricata*.

Source of variation	$F_{(DF)}$	<i>P</i>
Between-subjects		
Tagging	0.495 <sub>(1, 6)</sub>	0.507
Within-subjects		
Time	1.286 <sub>(4, 3)</sub>	0.435
Tag × time	2.186 <sub>(4, 3)</sub>	0.273

Repeated measurements (number of cockles eaten per day) were made on 5 consecutive days. Data were  $\ln(x + 1)$  transformed.

Mauchly criterion = 0.159, DF = 9,  $P = 0.524$ .

Bartlett test for homogeneity of variances ( $F = 0.661$ ,  $P = 0.744$ ).



**Fig. 2.** Cumulative number of shellfish (*Astrovenus stutchburyi*) eaten by tagged and untagged *C. muricata* in aquaria over 5 consecutive days.  $n = 4$  for each column.

was no significant ( $P = 0.507$ , Table 1) difference in the number of cockles eaten by tagged or untagged *C. muricata* (Fig. 2). Two-way ANOVA indicated that for both tagged and untagged sea stars, the time taken to right was significantly ( $P < 0.001$ , Table 2) faster at the start of the feeding trial compared with 5 days after feeding (Fig. 3). At both times there was, however, no significant ( $P = 0.659$ , Table 2) difference between tagged and untagged sea stars in righting rates (Fig. 3). In terms of *in situ* movement, no significant difference was detected in either the distance travelled ( $P = 0.687$ , Table 3A), or the depth ( $P = 0.299$ , Table 3B) of the tagged and non-tagged *C. muricata* 24 h after release (Fig. 4).

### 3.2. Effects of salinity on *C. muricata* activity

Sea stars placed in 15 PSU water died within 6 h of exposure, while treatment with 20 PSU seawater resulted in very low activity coefficients on initial exposure, and 100% mortality by 29 h (Fig. 5). Sea stars placed in 25, 30 and 34 PSU experienced no mortality during the 20-day trial period. Activity in these three treatments was variable over time, with no indication of changing activity rate with treatment duration. Among the salinity treatments, activity was almost always greatest in the full salinity treatment, and tended to decrease with decreasing salinity treatment. In this respect, the average ( $\pm$ SD) activity coefficient over all times pooled was  $4.02 \pm 1.46$  at 25 PSU,  $4.16 \pm 2.42$  at 30 PSU, and  $5.56 \pm 1.92$  in the 34 PSU salinity treatment. A repeated measures ANOVA indicated a significant difference in activity coefficient among salinities ( $P < 0.001$ , Table 4) but not days ( $P = 0.066$ , Table 4). A *post-hoc* test of differences among salinities indicated activity was significantly greater in the 25 to 34 PSU treatments compared with the lower salinities, but was not significantly different from 25 to 35 PSU.

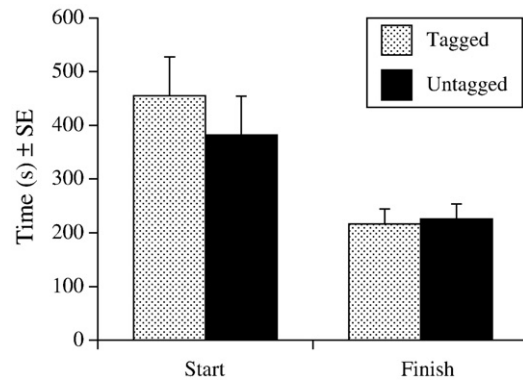
**Table 2**

Two-way ANOVA of the effect of tagging on righting time in *C. muricata*, immediately after tagging, and after a further 5 days.

Analysis of variance					
Source	SS	DF	MS	F-ratio	P
Model	0.712	3	0.237	8.159	<0.001
Error	1.047	36	0.029		
Total	1.761	39			
Effect of test					
Source	SS	DF	F-ratio	P	
Day	0.693	1	23.793	<0.001	
Tag	0.005	1	0.198	0.659	
Day $\times$ tag	0.014	1	0.488	0.489	

All data were  $\ln(x)$  transformed.

Bartlett test for homogeneity of variances ( $F = 0.319$ ,  $P = 0.8119$ ).



**Fig. 3.** Righting times of tagged and untagged *C. muricata* in the laboratory prior to the start of feeding trials, and after 5 days feeding in the laboratory.  $n = 4$  for each column.

### 3.3. Field deployment

Three of five tags were recovered in the field, with only one still attached to the sea star. The three tags collected data for a period ranging from 7 to 14 days. Over this time period, sea star movement was very dynamic in terms of vertical location (Fig. 6A), with sea stars altering their depth over several days. The sea stars ranged over a 5 m depth band between 0.39 m above MLW and 4.9 m below MLW (Fig. 6A), with mean depths of 2.22, 2.75 and 1.58 m for each individual respectively (Table 5). For *Sea star 1* and *Sea star 2*, the time spent at each depth (Fig. 7) was skewed to a deeper depth range, with both sea stars spending the majority of time (63% and 77%) at depths greater than 2 m, and approximately 10% of the time less than 1 m depth. *Sea star 3* showed a bimodal depth distribution, spending 57.8% of its time at depth shallower than 1 m, and 22.5% of its time at depths greater than 2.5 m. Interestingly, the movements of the sea stars were asynchronous, with shallow and deeper depths occupied by each sea star at different times (Fig. 6A). *Sea star 3* moved the least of the tagged sea stars, occupying shallow depths between 14 and 20 February followed by a movement to deeper depths for the remainder of the tagging period (Fig. 6A). Over the course of the tagging the sea stars moved a total vertical distance of between 53.3 and 178.7 m (Table 5), with the average vertical distance moved per day between 4.86 m and 14.15 m. Based on depths of the sea stars, the average vertical speed moved was similar for *Sea star 1* and *Sea star 2* ( $0.58 \text{ m h}^{-1}$  and  $0.51 \text{ m h}^{-1}$ ), although the maximum speed was higher in *Sea star 1* (Table 5, Fig. 8). *Sea star 3* moved at slower speeds during the study (see Table 5). If we take into account the vertical relief at Espinosa Point, the vertical distances based on depth recordings equate to approximately half the distance actually travelled. The sea

**Table 3**

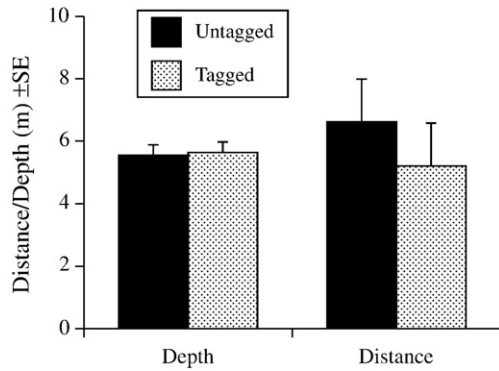
One-way ANOVA of the effect of tagging *C. muricata* on distance travelled (A) and depth located (B) 24 h after tagging.

(A) Distance					
Analysis of variance					
Source	SS	DF	MS	F-ratio	P
Tag	0.00428	1	0.0042	0.1707	0.6874
Error	0.2761	11	0.025		
Bartlett test for homogeneity of variances ( $F = 3.58$ , $P = 0.058$ )					
(B) Depth					
Source	SS	DF	MS	F-ratio	P
Tag	0.00199	1	0.0019	1.1857	0.2995
Error	0.0185	11	0.0016		

Data were  $\ln(x)$  transformed. Variances were heterogeneous for depth data, so comparisons were made using Welch ANOVA testing for equal means, allowing for unequal variances.

Bartlett test for homogeneity of variances ( $F = 6.79$ ,  $P = 0.0092$ ).

Welsh ANOVA testing mean equal ( $F(6.03, 0.28) = 1.372$ ,  $P = 0.2801$ ).

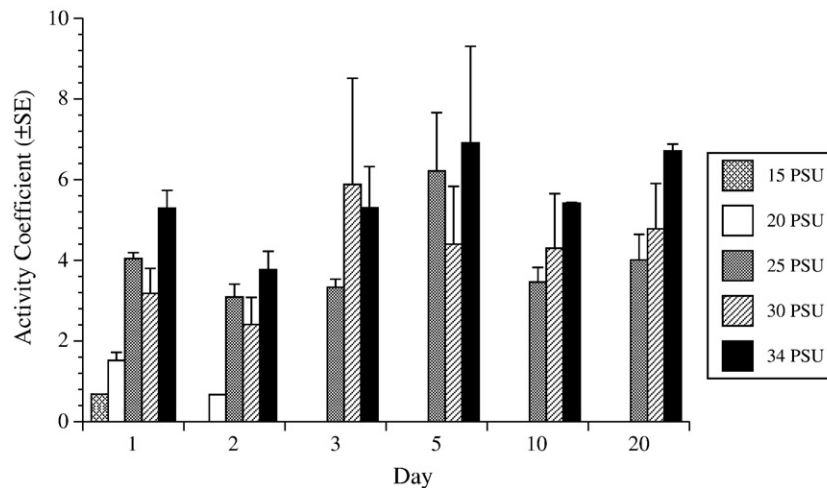


**Fig. 4.** Average depth and minimum distance travelled 24 hours after release of tagged and untagged *Coscinasterias muricata* in Deep Cove, Doubtful Sound.  $N=6$  for each column.

stars showed little horizontal movement over the course of the deployment; therefore, they are moving up to 10 to 28 m each day. If we take into account the 1:2 relief of the terrain, their speeds are also considerably higher and, in turn, approximately twice those shown in Table 5.

#### 3.4. The physical environment

A low-salinity surface layer (<28 PSU) occurred at Espinosa Point intermittently during the period of sea star tagging, with the depth of the 28 PSU halocline 3.2 m on 27 February (Fig. 9). Temperature and salinity were correlated (Fig. 9), with temperatures greater than 15.9 °C associated with seawater greater than 28 PSU. Over the course of the study, the LSL deepened markedly on the 25 February, with salinities <30 PSU at 4 m by the end on 26 February (Fig. 6A). The increase in the LSL can be attributed to an increase in rainfall toward the end of the study period (Fig. 6D), with a total of 114 mm falling between 23 and 27 February. Prior to this, no rainfall occurred between the 14 and 22 February. *Sea star 1* and *2* never occurred in water with salinities less than 28 PSU, with the two moving deeper during periods where the LSL increased in depth (i.e. 18 February and 23 February). During the period of the deep LSL and low surface salinities between 25 and 27 February, the remaining tagged sea star maintained its deep position between 4.5 and 5 m, which coincided with high salinity seawater. *Sea star 3* remained in shallow water during the first week of tagging, despite periods of lower salinity.



**Fig. 5.** Activity coefficients (righting time/1000) of *Coscinasterias muricata* exposed to five salinity treatments over a 20-day period. 100% mortality occurred in the 15 and 20 PSU treatment by day 1 and 2 respectively.  $N=3$  for each column.

**Table 4**

Univariate repeated measures ANOVA of activity coefficients of *C. muricata* among salinity treatments.

Source of variation	$F_{(DF)}$	$P$
Between-subjects		
Salinity	13.805 <sub>(4, 10)</sub>	<0.001
Within-subjects		
Time <sup>a</sup>	3.064 <sub>(2.09, 20.9)</sub>	0.066
Salinity × time <sup>a</sup>	1.333 <sub>(8.36, 20.9)</sub>	0.281

Repeated measurements of activity were made at six discrete times.

Mauchly criterion = 0.0045,  $DF = 14$ ,  $P < 0.001$ .

<sup>a</sup> Degree of freedom and  $P$ -value adjusted by Greenhouse–Geisser  $\epsilon = 0.418$ .

The temperature regime the sea stars experienced ranged from 13.6 to 17.5 °C over the course of tagging (Fig. 6B). Two of the sea stars (*Sea star 1* and *2*) experienced almost identical temperature regimes for the period of tagging overlap, with temperatures ranging between 15.5 and 17.5 °C. *Sea star 3* had a similar thermal history, although it experienced a period of lower sea temperatures between 17 and 20 February, with temperatures as low as 13.6 °C encountered. This likely reflects the closer proximity of this individual to the cooler low-salinity water within the LSL.

#### 4. Discussion

The foraging activity of sea stars can have an important role in structuring sessile marine communities, both in the intertidal (Menge et al., 1994; Menge and Branch, 2001) and subtidal (Witman and Grange, 1998; Gaymer et al., 2004; Himmelman et al., 2005). Fully understanding the ecological role of sea stars requires quantifying their foraging activity and feeding rate, such as prey selectivity and activity budgets of individuals during feeding (Gaymer et al., 2004; Himmelman et al., 2005). Monitoring sea star activity electronically presents a novel method for quantifying such movement and associated foraging activities over ecologically relevant time scales. *C. muricata* were tagged with small electronic archival tags to examine aspects of their distribution and movement. The validity of field data will depend on the effect tagging has on the animal. We could not detect any change in either the behaviour of tagged animals versus control animals, either in terms of feeding rates or movement over a 24-hour period. Similarly, tagging by piercing the sea star arm did not appear to have a detrimental effect on the fitness (as measured by righting time) either immediately following tagging, or after 5 days of tagging. The relocation of a healthy, tagged sea star from the field two

**Table 5**  
Summary of vertical position and movement dynamics of sea stars over the tagging period.

	Sea star 1	Sea star 2	Sea star 3
Days tagged	7.0	13.6	11.0
Mean depth	2.22 m	2.75 m	1.58 m
Maximum depth	3.48 m	4.9 m	3.93 m
Minimum depth	0.22 m	+ 0.39 above MLW	+ 0.06 above MLW
Total vertical distance moved	99.1 m	178.7 m	53.3 m
Average daily vertical distance moved	14.15 m	13.14 m	4.86 m
Average speed	58 cm h <sup>-1</sup>	51 cm h <sup>-1</sup>	20 cm h <sup>-1</sup>
Maximum speed	23.3 m h <sup>-1</sup>	19.2 m h <sup>-1</sup>	1.78 m h <sup>-1</sup>

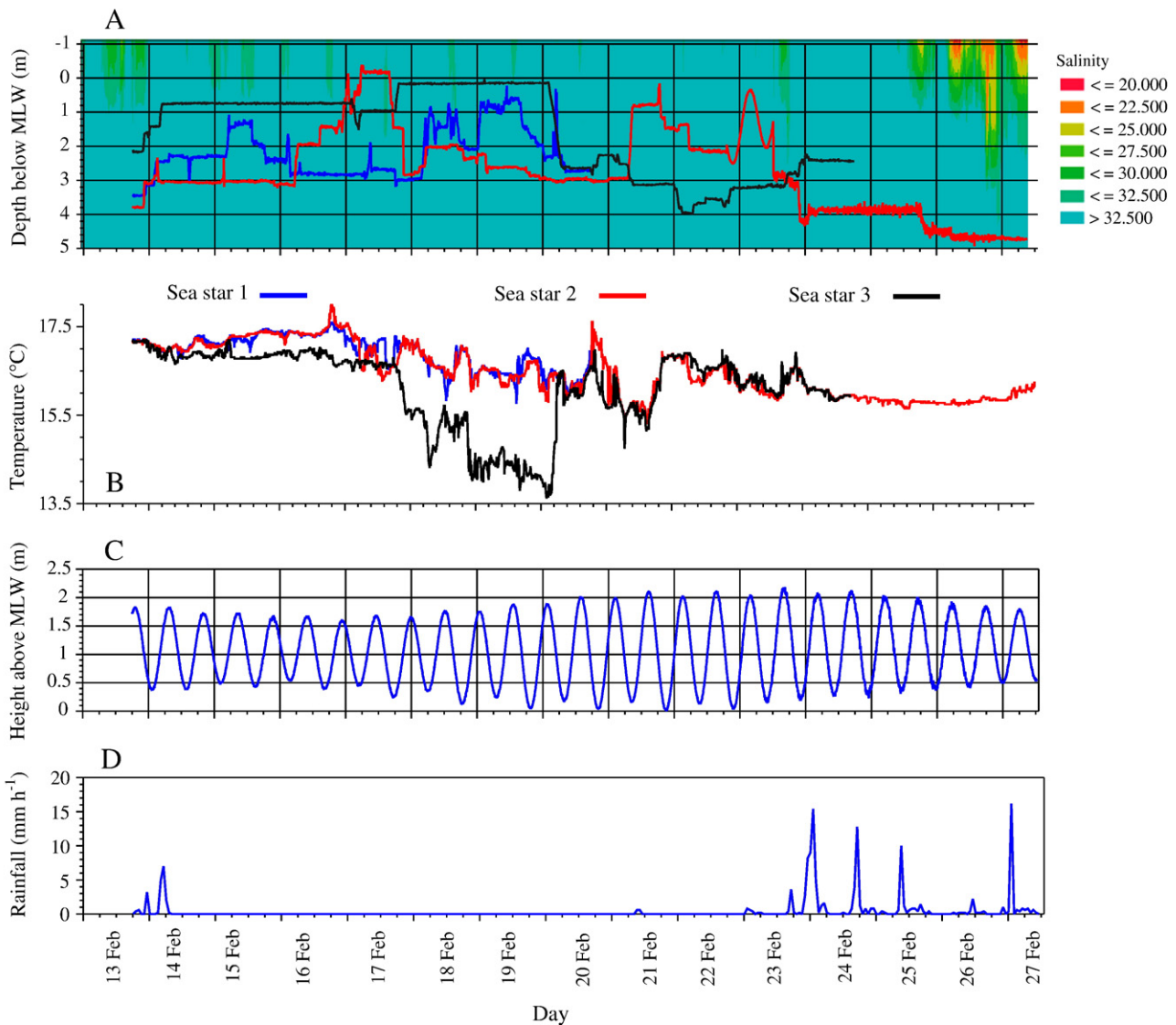
weeks after tagging provides further evidence that the tagging process was relatively benign.

Tags were fully retained in the laboratory; however, two tags were removed from sea stars in the field during the tagging trials and two were not able to be recovered. These results suggest that there are mechanisms in the natural environment that reduce tag retention. Possible mechanisms include the removal of tags by fish or

inadvertent removal by scraping of the tags against rough landscape features such as rocks and crevices. The fact that two of the dislodged tags were still able to be relocated highlights the importance of conducting these types of tagging studies in areas that have ledges or flat terrain below the area of deployment.

The primary aim of this study was to test the utility of electronic archival tags in examining the ecology of a subtidal marine invertebrate such as *C. muricata* as apposed to more conventional methods such as direct observations. Quantitative observations can provide information on the spatial distribution of sea stars, but these are typically at discrete times, and most often at the population level. In contrast, electronic archival tagging like that used in this study provide continuous, fine time-scale, quantitative information on sea star activity such as the vertical position, vertical direction and rates of movement at the individual level. The data collected on *C. muricata* shows the potential of electronic tagging as a powerful tool for understanding behavioural ecology of sea stars and other foraging benthic invertebrates beyond that possible from discrete observations. We use foraging activity and environmental influences on their movements as examples.

Foraging strategies, and their optimisation, have been examined in sea stars extensively (i.e. Menge, 1972), with the aim of understanding



**Fig. 6.** Change in the vertical position relative to MLW of tagged sea star (A). The temperatures logged by each sea star over the same period are given (B). Positions and temperatures were recorded every 5 min. Tidal height above MLW (C) and rainfall data (D) for Espinosa Point, Doubtful Sound is given for the two-week period of tagging.

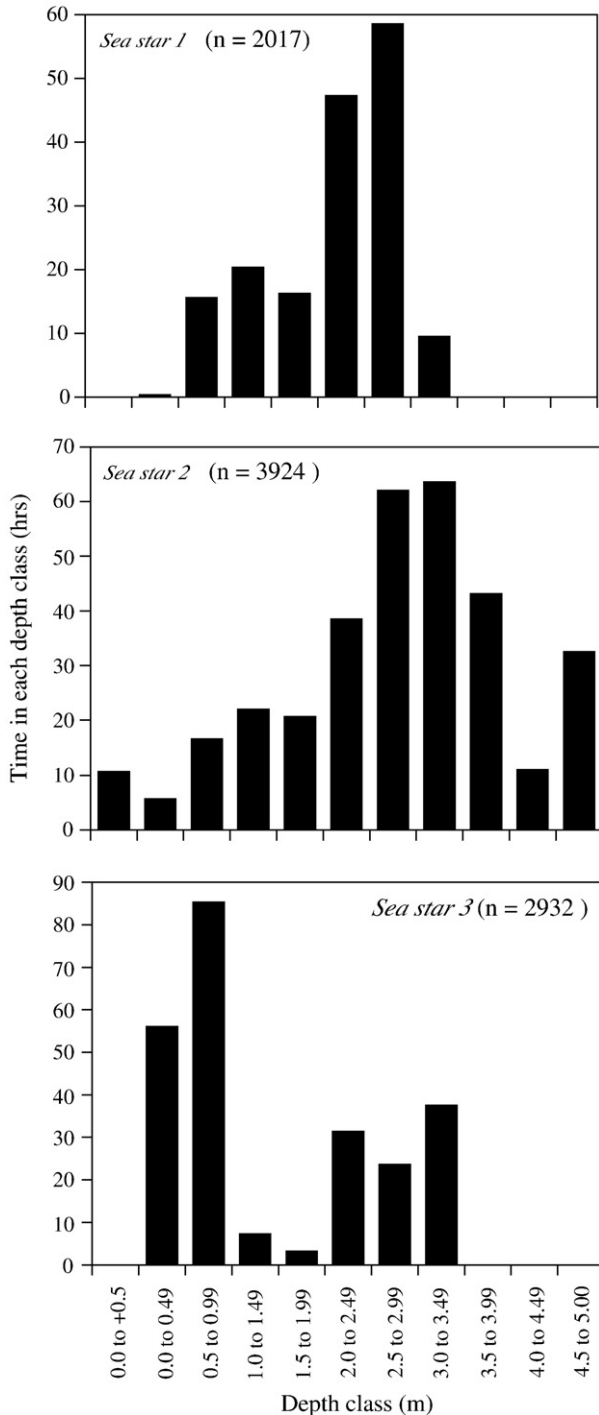
the role of prey selection and distribution (Himmelman and Dutil, 1991), physical drivers (Rochette et al., 1994; Witman and Grange, 1998; Barker and Russell, 2008), energetics (Menge, 1972), and inter- and intra-specific competition (Menge and Menge, 1974; Gaymer et al., 2002) during feeding. Electronic tagging of individual sea stars provide a direct quantitative method of exploring relatively complex and variable details of foraging activity, such as where and how often they feed, how feeding strategies vary spatially and temporally (in relation to spatial variability in food and changes in energetics), and

how much movement may be occur during foraging. Importantly, variability among individuals in foraging can be quantified, such as between sizes and sexes.

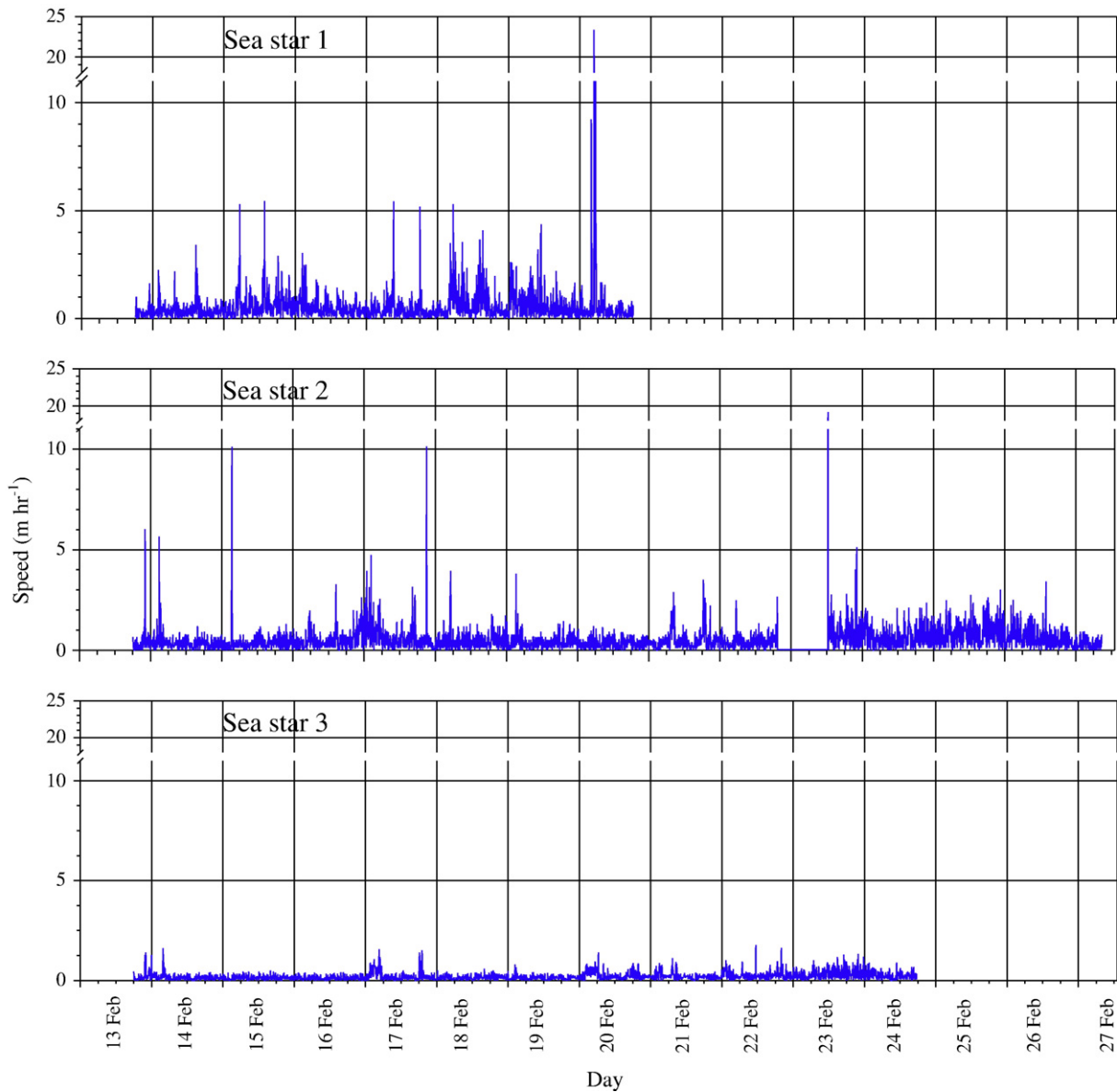
*C. muricata* in New Zealand fiords feed almost exclusively on blue mussels found within shallow waters (Clarke, 2002), which provide some refuge from predators due to the frequent presence of buoyant low-salinity layers (Witman and Grange, 1998). The movement of *C. muricata* into shallow water likely represents a foraging associated activity. For example, our direct observations indicated that the percentage of sea star feeding was 92% ( $n = 98$ ) in water less than 1 m, 12% ( $n = 88$ ) between 1 and 3 m depth, but only 9% ( $n = 100$ ) in sea stars at depths between 3 and 5 m (M. Lamare, unpublished data). From their vertical position we can therefore estimate the percentage of time each individual spends in contact with their preferred food (and hence the percentage of the population). The average percentage of time spent in shallow water (<1 m above MLW) was  $\approx 26\%$  among the three sea stars, which would could potentially mean approximately a quarter of the population are feeding at any one time. Himmelman and Dutil (1991) found a similar percentage of the population feeding in *Lep-tasterias polaris*, but lower for the larger *Asterias vulgaris* (10 to 11%). Vertical movement of the three tagged sea stars contrasted, and suggest that foraging activity is relatively variable at the individual level. *Sea star 1* and 2 tended to occupy deeper water below the mussels, and migrated into shallow water to feed for relatively short periods (<day), and at intervals of approximately 5 days. In contrast, *Sea star 3* occupied shallow depths for the first week of tagging before moving to sub-mussel depths for the remaining 4 days of tagging.

The ability of mobile invertebrates to forage within the shallows is also influenced by physical factors such as waves and the presence of low-salinity layers (Witman and Grange, 1998; Siddon and Witman, 2003). Hence, the application of electronic tags to benthic invertebrates such as echinoderms allows for movement behaviours to be observed over time periods relevant to physical oceanographic processes. Electronic tagging of sea stars can be used to quantify the influence of the physical environment on their behaviour, both directly by logging physical parameters on the tag itself, and indirectly if their activity is correlated with concomitant measurements made on the physical environment. *C. muricata* tagging provides examples of both. In Doubtful Sound, water temperature is often correlated with salinity, and the temperature data logged by the sea stars can be used as proxy of salinities the sea stars encounter. During the 2 weeks of the tagging lower salinity water (<28 PSU) had a temperature of less than 15.8 °C. The temperatures logged by *Sea star 1* and 2 were almost always above this temperature indicating they remained in full salinity water, even during fluctuating surface salinities. In contrast, *Sea star 3* logged temperatures less than 15.8 °C during a period when it occupied shallow water indicating a period of exposure to lower salinity water for a period of 2–3 days. Comparing vertical distributions of *C. muricata* with salinity profiles over the course of the study was less interesting due to the lack of rainfall over the sampling period. Salinities remained relatively high, with the exception of the last three days of the study, when lower salinities (<30 PSU) penetrated down to 3 m. During this deepening of the low-salinity layer (LSL), the single remaining tagged *Sea star 2* moved to its deepest position between 4 and 5 m and beneath the layer of low-salinity water. While this response is based on a single observation, it supports previous studies that have observed *C. muricata* to aggregate beneath the influence of the LSL (Witman and Grange, 1998; Clarke, 2002).

The field observations are consistent with laboratory observations that indicate that *C. muricata* cannot tolerate exposure to reduced salinities (<25 PSU), with 100% mortality occurring within 6 h exposure to 15 PSU and within 29 h if exposed to 20 PSU. The ability of *C. muricata* to tolerate a degree of lower salinity (i.e. down to 25 PSU) is consistent with previous observations (Shamuyu, 1977; Forcucci and Lawrence, 1986; Stickle and Diehl, 1987; Barker and Russell, 2008), but shows that the low salinities found at the sea surface of



**Fig. 7.** Time spent in 0.5 m depth classes between 0.5 m above MLW and 5 m below MLW for two sea stars over a 7-day period (*Sea star 1*), 11-day (*Sea star 3*), and a 13-day period (*Sea star 2*).



**Fig. 8.** Vertical speeds of tagged sea stars over a 7 to 14-day period. Instantaneous speed (given in  $\text{cm hr}^{-1}$ ) was calculated from the change in vertical position over each 5 minute logging period. Note that there are y-axis breaks in all figures.

Doubtful Sound could not be tolerated by *C. muricata* for any length of time.

These observations highlight the need for *C. muricata* to regulate its vertical distribution in response to changes in surface salinities, (which ranged from 11 to 34 PSU during the period the tagging). Interestingly, it appears as though the animal began its descent prior to the deepening of the LSL at Espinosa Point, which would suggest that other physical cues such as changes in wave action associated with increased winds may also be playing a role in their vertical distribution. Rainfall is typically accompanied by strong up-fjord winds that set up the freshwater at the head of the fjord and cause a deepening event; hence the thickening of the LSL at Espinosa point is lagged behind the beginning of the rainfall (Gibbs, 2001). An increase in wind-induced wave action at the beginning of the rainfall is suggested by a corresponding increase in noise in depth measurements on both the tag on *Sea star 2* and the tag being used as a tide gauge.

The ability of *C. muricata* to avoid low-salinity exposure during a deepening event is consistent with vertical speed measurements that

indicate *C. muricata* can move faster than the rate at which the LSL deepens. For example, the rate at which the LSL deepens during weather events is on the order of  $0.5 \text{ m h}^{-1}$ , while the rates of *C. muricata* vertical movement observed in the present study were estimated between 1.78 and  $23.3 \text{ m h}^{-1}$ . If we take into account the 1:2 relief of the terrain at Espinosa Point (see Fig. 1), their actual rate of movement is about twice as high as these estimates, meaning that they can move considerable distances over a relatively short time period in response to both physical and chemical cues. Our estimates of vertical movement for *C. muricata* (see Table 1) are comparable with an average of 3.9 m over a 6 h period (i.e.,  $15.6 \text{ m day}^{-1}$ ) measured for the same species by Witman and Grange (1998), but considerably faster than those measured for other sea stars ( $2.3$  to  $4.3 \text{ m day}^{-1}$  for *Acanthaster planci* (Keesing and Lucas, 1992),  $1.5$  to  $3.7 \text{ m day}^{-1}$  for *Asteria pectinifera* (Kurihara, 1999), and an average of 1.42 m over 6 h (i.e.,  $5.7 \text{ m day}^{-1}$ ) in *Patriella regularis* (Witman and Grange, 1998s)).

The research presented here introduces the strong potential of using archival electronic tags for studying movement behaviour in a foraging



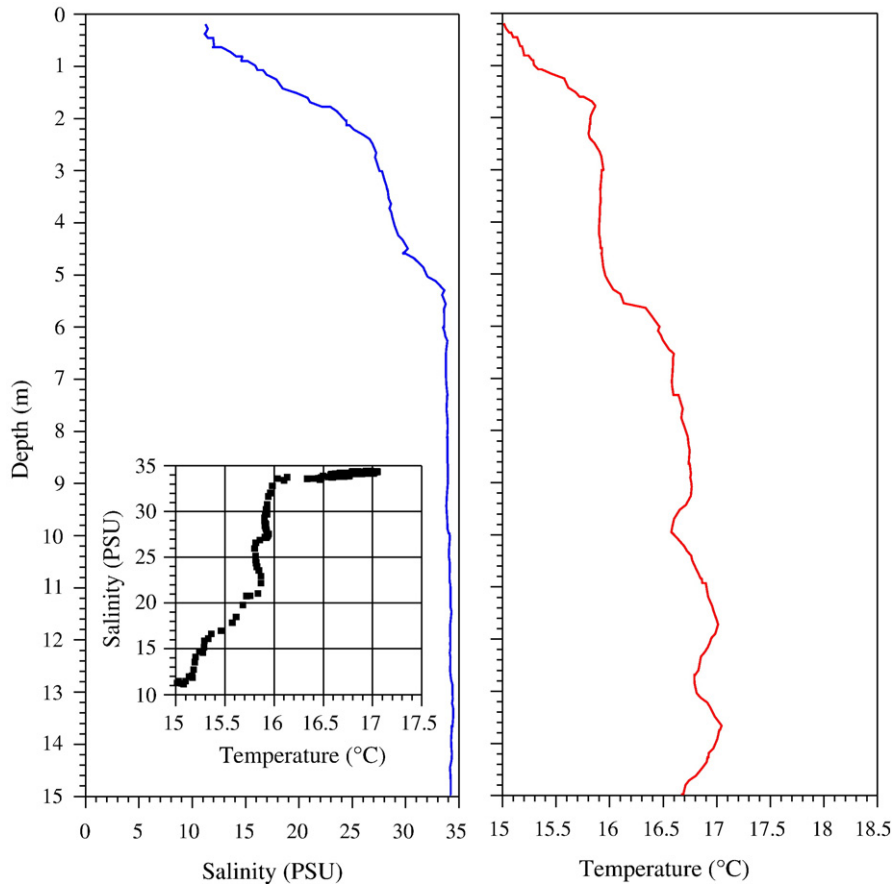


Fig. 9. Salinity temperature profiles for Espinosa Point, Doubtful Sound on 27 February 2008. The insert figure is the temperature/salinity plot for the water column from 0 to 15 m.

benthic invertebrate. This paper was not intended as a detailed study on *C. muricata* behaviour, although we have highlighted the utility of the technique through a brief discussion of the application of tagging data for understanding sea star behaviour and their response to the physical environment. Coupling these sets of data opens up the ability to quantitatively understand the role of the physical environment in driving ecology processes, directly for the species of interest, but also indirectly by understanding how the physical environment influence keystone species and habitat modifiers. Despite its expense, future research with small archival tags should advance our quantitative understanding on the behavioural ecology of invertebrate species with a large vertical range, high degree of mobility and nocturnal activity (i.e. larger crustacean species, octopus).

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